Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

SEVENTEEN YEARS SELECTION OF A CHARACTER SHOWING SEX-LINKED MENDELIAN INHERITANCE[1]

RAYMOND PEARL

I

IN 1898 there was begun at the Maine Agricultural Experiment Station an experiment in breeding Barred Plymouth Rock fowls, having for its purpose the improvement by selection of the character winter egg production. This investigation has continued to the present time. A résumé of the results to date, considered with reference to their bearing upon the general biological problem of selection, may be of some interest.

The experiment has fallen into three divisions or periods: viz., (1) the period from 1898 to 1907, (2) the period from 1908 to 1912, and finally (3) the period from 1912 to date. Detailed reports on the methods of breeding in operation have been published elsewhere.[2] For purposes of clear orientation in the present discussion it will be well here briefly to review the facts as to the methods of breeding used in each of the periods. With these facts definitely in mind we may then proceed to an examination of the results.

1. *The Period from 1898 to 1907.*—During this period the breeding followed the plan outlined at the beginning by Woods and Gowell. Essentially it consisted of the following elements.

1. Trap-nest record of the performance of each individual female.
2. Selection as breeders of all females which laid more than a definite number of eggs (150) in the first laying year.

---

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 87.

[2] Cf. particularly Woods, C. D., and Gowell, G. M., U. S. Dept. Agr. Bur. Anim. Ind. Bulletin 90, 1906, pp. 42; Pearl, R., and Surface, F. M., *Ibid.* Bulletin 110, Part I, 1909, pp. 80; Pearl, Me. Agr. Expt. Stat. Ann. Rept., 1911, pp. 113–176; and Pearl, *Jour. Exp. Zool.*, Vol. 13, 1912, pp. 153–268.

3. Selection as breeders of males whose dams had laid more than another definite number of eggs (200).
4. The indiscriminate mass breeding, *without* individual pedigrees, of all individuals selected as described under 2 and 3, and, in consequence,
5. *No test of the progeny* of particular matings with respect to their laying ability.

This may be designated as the *period of mass selection.*

The following statement regarding the methods used in this period was made by Woods and Gowell (*loc. cit.*, p. 8):

> The plans followed in this breeding work are based upon everyday, practical common sense, and are the same as would be used in building up a high-producing strain of dairy animals. Individual records of performance are kept. The large producers are mated with sons of large producers in the hope of obtaining a race of improved layers. In the first year's work three birds laid over 200 eggs each, and this fact led to the adoption of that number of eggs as the minimum performance for a "registered" bird. Other than this there was no reason for selecting 200 as the number of eggs necessary to entitle a bird to registration. Any other number, as 190 or 210, might have been taken with equal propriety, just as horsemen might have selected some other time than 2.30 by which to determine a standard horse.

2. *The Period from 1908 to 1912.*—For reasons which have been fully set forth elsewhere[3] it was decided not to continue the breeding along the same plan after 1907. The new plant, put into operation first in the breeding season of 1908, was calculated primarily to furnish definite information regarding the mode of inheritance of the character winter egg production. It involved essentially the following items:

1. Trap-nest record of the performance of each individual female.
2. The selection of both males and females was made on a *double* basis, including in addition to the individual's own performance as in the earlier plan, also the idea of progeny performance. In practice this worked out *for hens* in the following way: Plans were made to see whether there could

---

[3] Pearl and Surface, *loc. cit.*

be formed by selection and propagated three distinct strains of winter egg producers, namely, high, mediocre and low. This involved, *on the individual performance side,* the separate selection in the first years of *three* classes of females as breeders: (*a*) good winter producers, with records before March 1 of above 30 eggs; (*b*) mediocre winter producers, with records below 30 eggs; and (*c*) poor winter producers, which laid no eggs before March 1. The division at 30 eggs was, after the first year, merely a nominal one in the selection of *high* producers. Actually only birds were used in the *a* class whose records materially exceeded 30 eggs, running up to over 100 eggs in some cases.

The *progeny performance* idea was carried out in two ways in the breeding. In the first place, no female was selected for the *high* winter production breeding pens, for example, unless, in addition to her own high winter record, all her sisters and her dam were high producers. In the second place, of all females fulfilling the above qualification only those were bred a second time whose progeny from the first year's mating had proven to be all high producers. Similar types of selection were followed by the mediocre and low lines, except that segregating families were put in the mediocre class.

3. The selection of males was along essentially the same lines, with only such difference as is involved in the fact that the male makes no performance record himself. Males were put into the breeding pen the first time on the basis of the records of their dams, on the one hand, and of their sisters, on the other hand. Those whose progeny proved that they were transmitting the character to which selection was being made were used a second or even third time as breeders.
4. Complete individual pedigrees, whereby each off-

spring individual's parentage, both male and female, was known.

5. The records of production of the progeny of each mating separately recorded and studied as a unit.

It will be noted that there are but two essential differences between the plan in this period and that followed in the earlier one. These are: first and most important, that in this second period the principle of *progeny testing* was introduced into the scheme of breeding. The second difference was that selection was carried on for low production as well as for high, which had not been previously done. A third difference is apparently found in the fact that in this second period of selection the winter record rather than the yearly record is made the basis of selection. This is in no way an essential difference. The reasons for adopting the winter period have been set forth in detail elsewhere[4] and need not be repeated. It suffices to say here that essentially the same results and conclusions will be reached if one uses winter production or annual production.

As a result of the studies made in this period on the plan of breeding outlined the mode of inheritance of the character winter production was definitely determined, and has been confirmed by subsequent work.[5] The character was shown to be Mendelian in its genetic behavior, depending upon two factors, one of which is sex-linked.

3. *The Period from 1912 to Date.*—The only difference in the mode of breeding the stock of Barred Plymouth Rocks in this period, as compared with the preceding one, is found in the fact that during this last period *all selections for low and mediocre production have been dropped.* The breeding for high production alone continues, with only such differences in the details of manipulation of the breeding stock as would naturally follow a definite knowledge of the mode of inheritance of the character,

[4] Pearl, 1912, *loc. cit.*, and Me. Agr. Exp. Stat. Ann. Rept., 1914, pp. 217–236. Cf. also Wilson and Murphy, *Jour. Dept. Agr. Ireland*, Vol. XIV, No. 2.

[5] Pearl, 1912, *loc. cit.*, also AMER. NAT., Vol. XLIX, 1915, pp. 306–317, and Curtis and Pearl, *Jour. Exp. Zoology*, Vol. 19, 1915, pp. 45–59.

and of the gametic constitution of particular individuals with reference to that character. As a matter of fact, all low-producing lines were dropped at the end of the laying year 1911–12. Certain of the mediocre lines were continued a year longer. In the laying flock of 1913–14 there were no birds which had been bred for anything other than high production, so far as the breeder's deliberate intention went.

II

The results of this seventeen year selection period are set forth in Table I.

TABLE I

Mean Winter Production Per Bird of the Barred Plymouth Rock Flocks from 1899 to 1915

Laying Year	Mean Winter Production of All Birds	No. of Birds Making Winter Records	Mean Winter Production of All Birds Selected for *High* Production	Mean Winter Production of All Birds Selected for *Low* Production
1899–1900	41.03 eggs	70	—	—
1900–1901	37.88 "	85	—	—
1901–1902	45.23 "	48	—	—
1902–1903	26.01 "	147	—	—
1903–1904	26.55 "	254	—	—
1904–1905	35.04 "	515	—	—
1905–1906	40.65 "	635	—	—
1906–1907	22.44 "	653	—	—
1907–1908	19.93 "	780	—	—
1908–1909	26.69 "	359	54.16	22.06
1909–1910	31.76 "	247	47.57	25.05
1910–1911	30.49 "	264	50.58	17.00
1911–1912	35.93 "	232	57.42	16.43
1912–1913	43.01 "	182	52.61	—
1913–1914	52.20 "	192	52.20	—
1914–1915	45.89 "	179	45.89	—
Totals and means	35.05 "	4,842	51.49	20.14

The data of this table are shown graphically in Fig. 1.

From the table and diagrams the following results appear:

1. The number of individuals involved in this experiment, on each one of which exact trap-nest records have been kept, is large, amounting nearly to five thousand. This number is large enough to lead to conclusions which are trustworthy. It will be shown presently that wherever it has been possible to compare the results on egg produc-

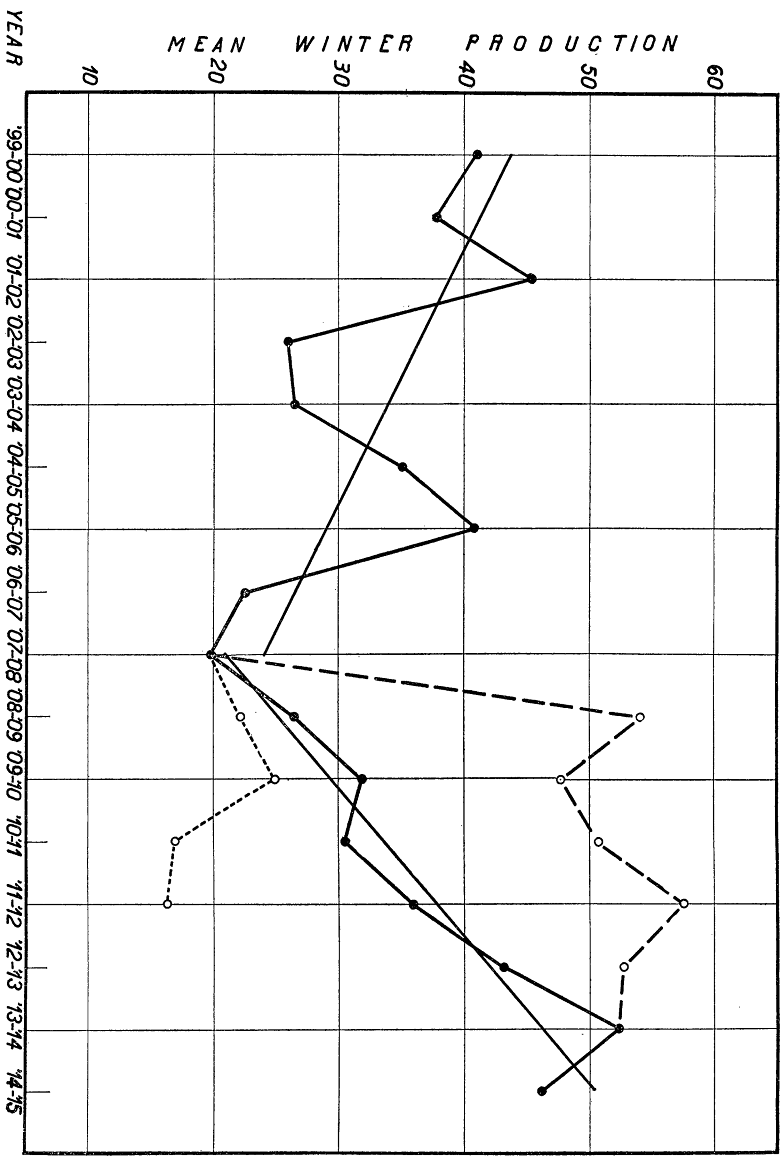

FIG. 1. Graph showing the course of mean winter egg production between the years 1899 and 1915. The solid lines and circles give the total flock means. The two straight lines, fitted by the method of least squares to the observed flock means, have the equations, $y = 43.655 - 2.181x$, and $y = 17.070 + 4.148x$. The open circles and broken (dash) line give the means of the lines selected for high winter production between the years 1908 and 1915. The dotted line and open circles give the mean winter production of the lines selected for low production between the years 1908 and 1912.

tion obtained in this experiment with independentl termined norms the general trustworthiness and normality of the present data have been demonstrated.

2. From the beginning of the experiment through the laying year 1907–08 the general trend of mean production was downward, with minor fluctuations from year to year. In other words during the period in which the system of breeding was mass selection for high production without progeny test there was no change of the mean in the direction of the selection. The fluctuations in mean production during this period were, in the main, due probably to two sets of causes: (*a*) environmental differences in different years acting at one point or another in the life history of the birds; (*b*) random fluctuations in the genetic constitution of the male birds used as breeders in successive years, brought about because of the ignorance of the breeder, in the absence of any individual progeny testing plan, of the ability of any particular male to transmit high fecundity to his daughters. The first of these factors needs no special discussion and is relatively of minor importance. The second will be dealt with in detail farther on in the paper.

3. Since the laying year 1907–08 there has been a steady increase in mean winter production for the whole flock, except for the years 1910–11 and 1914–15. In the former year the decline in the mean is slight, and is probably due to unfavorable environmental influences. In 1914–15 the decline is certainly due to such causes. In the hatching season of 1914 an inexperienced man was in charge of the incubation and rearing. He had very poor success, and the Barred Plymouth Rock pullets available for the laying houses in the fall were relatively few in number, of a relatively late average date of hatching, and poorly grown. It is remarkable, not that the mean winter production was lower in 1914–15 than in 1913–14, but rather that it was so high as it was, taking all the circumstances into account. It appears that the system of breeding which made the selections on a progeny test basis was immediately and, to date, continuously effective.

4. That selection on a progeny test basis was effective is demonstrated not only by the general flock averages, but also by the fact that it was possible to propagate separately high and low producing strains. The high producing strains differed widely from the low producing in mean winter production. Taking the average for seven years in the case of the high, and four years in the case of the low, it appears that the mean winter production of the high producing strains was approximately two and a half times that of the low producing strains. At the end of the laying year 1911–12 the low producing lines were dropped. In the next year (breeding season of 1913) no birds were bred which were known to belong to segregating lines. Of course some were included which proved afterwards to have been segregating, but this fact could not, in any such case, have been told in advance from the records in hand. The propagation of low producing strains was attended with a great deal of practical difficulty with the environmental conditions under which one has to operate at this station. The growing season is short. In order to grow properly a pullet for laying purposes it is necessary that she be hatched after April 1 and before June 1 *at the latest,* and preferably before May 15. If, however, one selects birds which produce no eggs whatever before March 1, and use up some valuable time before they get well started in the spring cycle of laying it becomes perfectly clear that one is automatically prevented from getting any considerable number of early hatched chicks from such mothers. If late hatched chicks are used the results obtained as to winter production later will not be critical. These circumstances make the propagation of a low producing strain on a large scale really a difficult proposition. There is of course no difficulty in breeding birds which will not be winter layers. One only needs to hatch in June, July or August. But such birds will furnish no critical evidence regarding the inheritance of winter production.

5. The mean winter production for whole flocks over the entire period of the investigation is 35.05 eggs. In

the writer's opinion, based upon rather extended experience in the study of egg records, approximately this figure may be taken as representing the general average winter production of mixed flocks of Barred Plymouth Rocks (or of American birds generally with the probable exception of White Wyandottes), which have been hatched at the proper time and well reared. As evidence on this point the data presented in Table II have pertinent bearing. These data give the mean winter production of birds of the different American breeds obtained in the Fourth Philadelphia North American International Egg-Laying Competition, carried on at the Delaware Agricultural Experiment Station in 1914–15. The conditions under which these records are made are such as to safeguard their essential accuracy. The figures here given are the mean productions per bird up to the end of the eighteenth and seventeenth week of the laying after November 1, 1914. Owing to the fact that the original records as published are compiled by calendar weeks it is not possible to give the exact production from November 1 to March 1. Eighteen weeks gives 5 days laying over this period, and seventeen weeks gives 2 days under. Both sets of means have therefore been tabled. It should be said that the birds were kept in flocks of 5 birds each, thus tending to the most favorable condition for high individual records.

TABLE II

MEAN WINTER PRODUCTION OF FOWLS OF THE AMERICAN BREEDS, CALCULATED FROM RECORDS OF THE FOURTH INTERNATIONAL LAYING COMPETITION, 1914–15

Breed	No. of Birds	Mean from Nov. 1 to Mar. 5	Mean from Nov. 1 to Feb. 26
Barred Plymouth Rocks......	45	29.20	25.47
All Plymouth Rocks..........	80	32.39	28.39
All Wyandottes................	55	48.20	44.00
All Reds..........................	75	38.37	34.42
All American breeds..........	210	38.67	34.63

From this table it is clear that the records presented in Table I average about the same as those of the 210 birds of the American breeds in the Delaware competition, The Wyandottes alone give a distinctly higher mean, and this the writer has also found to be true of Irish egg records. The Barred Rocks in the competition this year give a somewhat abnormally low winter mean. Irish records[6] give a winter mean for 48 Barred Rocks, in flocks of 6 each, of 36.54 eggs per bird which is more nearly normal.

III

Let us now turn to the question of the interpretation of the data set forth in the preceding section. Broadly speaking what the facts gleaned from this seventeen-year experiment show is that mass selection for egg production was *not* effective, while selection which was based upon the performance of the progeny *was* extremely and quickly effective. What is the explanation of the difference? The facts are purely objective realities, about which dispute or question is idle. They are real and obvious matters. Regarding the interpretation of such facts as these there have been, and no doubt will continue to be for some time to come, differences of opinion amongst biologists. Under these circumstances, the writer will, then, with all respect and consideration for the differing opinions of others endeavor to make clear the view of the meaning of these results which he has come to hold.

In the first place we may definitely put aside any interpretation which bases its explanation of the results on environmental action. In an earlier paper the writer[7] has shown in detail the impossibility of this explanation for the results during the period of mass selection (the descending limb of the curve). The totality of the results here presented make it still more apparent that such an explanation can have no place here. We should have to suppose that the environmental influences were adverse throughout the period of mass selection, but suddenly became favorable when the method of breeding was changed, and have ameliorated at an ever increasing rate as time has gone on. Nothing of the sort was, in fact, the case. The only explanation which can satisfy the case is one which is based upon or at least takes full account of the changing genetic constitution of the flock.

---

[6] Murphy, L., *Jour. Dept. Agr. Ireland,* Vol. XIV, pp. 8–30, 1913.

[7] Pearl, R., Me. Agr. Expt. Stat. Ann. Rept., 1911, pp. 113–176.

It appears to the writer that the essential key-note to the explanation of the results of this long experiment is found in the fact that *phænotypic variation of the character fecundity, in fowls, markedly transcends, in extent and degree, genotypic variation.* It is quite impossible in the great majority of cases to determine with precision what is a hen's genetic constitution with respect to fecundity from an examination of her egg record *alone*. In this case, as in so many others, but in an unusually pronounced degree, where the phænotypic distributions overlap, a sure diagnosis of genetic constitution can only be made by means of the progeny test. Lacking this the phænotypic performance becomes an always uncertain and at times very misleading guide.

It can be shown that if, during the period of mass selection, all the hens used as breeders had been, as they were supposed in the theory of the originators of that part of the experiment to be, either Type 1 or Type 2 females ($fL_1L_2 \cdot \widehat{Fl}_2l_1$ or $fL_1L_2 \cdot \widehat{Fl}_2L_1$) then the continued mass selection must have resulted in improvement. The *only* criterion of constitution which was used, however, was the bird's performance. But, taken by this criterion alone, there would be constantly chosen a proportion of birds whose genotype was for mediocre fecundity, but which made a performance record (phænotypic) sufficiently high to be selected. That this is what actually happened is evident from the curve (Fig. 1), but the fact was experimentally proved in 1909.[8]

Put in the fewest words, then, the reason why no effect was produced during the first ten years of selection and a marked effect was produced during the last seven, was, in the writer's opinion, because genotypically high producers were *uniformly* selected (in the high lines) during

[8] Pearl and Surface, Me. Agr. Expt. Stat. Ann. Rept., 1909, pp. 49–84.

the latter period, and were *not* uniformly selected in the former. By the introduction of the progeny test as an essential part of the selection the whole process of the creation of a highly fecund race of hens was transferred from the realm of blind chance to that of precise and definite control. And it becomes increasingly clear that mass selection, on the basis of performance (phænotypic appearance) alone, is in its essential nature a blind and haphazard process, no matter with what precision and stringency it is carried out, just so long as the correlation between the gametic and somatic conditions of the character selected is not perfect. And it is an outstanding result of the Mendelian investigations of the last 15 years that the gamete-soma correlation is very rarely, if ever, perfect.[9]

It appears on this view that selection for high egg production in the fowl is effective when it is real. That is, if one selects *genetically* high producers by means of the trap-nest *plus* the progeny test, he succeeds very rapidly in fixing a high producing strain. If on the other hand he merely selects high layers by the trap-nest record alone, he is not really selecting genetically high producers except in a portion of the cases. Under these circumstances he makes no progress in building up a highly fecund strain. To be effective in changing the average productiveness of a flock of poultry selection must pick out those birds as breeders which carry the factors for high fecundity genetically, *i. e.*, as an integral part of their hereditary make-up, *and not any other birds.*

With the above interpretation of the results of seventeen years' continuous selection of the character fecundity, *all the facts known to the writer are in complete accord. No other interpretation of the results of this experiment* has yet been suggested which will meet all the facts.

---

[9] Complete citations on this point would make a tolerably full bibliography of Mendelism. The methodological or the strictly quantitative aspects of the problem have been but little dealt with. In this connection cf. W. F. R. Weldon, *Biometrika,* Vol. I, pp. 228–254, 1902, and R. Pearl, *Biol. Bulletin,* Vol. XXI, pp. 339–366, 1911.

IV

What bearing have these results upon the general problem of the effectiveness of selection in modifying germinal determiners? Let us at the outstart endeavor to be quite clear as to the problem. It has been shown in what has preceded that in the long experiment a change in the average condition of the population has occurred, and has been coincident with selection. The writer has no hesitation in saying that the increase in average productiveness since 1908 has been *caused* by the particular kind of selective breeding practised. Furthermore the average productiveness at the present time transcends any average known in the previous history of the stock.

Granting all this, however, as plain matter of fact, it does not, in the writer's opinion, afford one iota of evidence that through the process of selection the hereditary determiners of fecundity either have been or can be changed. All that the selection has done, so far as we have any evidence, is to change the constitution of the *population* in respect of fecundity genotypes. There is no evidence that the genotypes themselves have been changed. On the contrary, everything indicates that they have not been changed. During the last seventeen years we have merely sorted out from a mixed population, by a systematic method of breeding, those individuals which were alike in one respect, and have sold all the rest to the butcher. That one respect was that each individual bore progeny which were high producers.[10] Those individuals chosen as breeders in 1908 and 1914 were precisely alike in this particular There were more of them available in proportion to the whole flock in 1914 than in 1908, but, as individuals, I am unable to discern any particular in which they were different in 1914 from what they were in 1908.

The general point here involved is essentially the same as one with which we are more familiar in demographic statistics. The constitution of a population does not directly affect the individual. My expectation of life will not be materially increased if I chance to move into a community in which all the other inhabitants are of advanced age. To this everyone will agree. But the extreme selectionist appears to believe that in some mysterious way the act of continued selection, which means concretely only the transference of each selected individual from one cage or pen to another to breed, will in and of itself change the germ-plasm, so that after the act it is different from what it was before! It does not seem that the evidence that such is in fact the case is critically valid. A careful study of the very interesting and valuable work of Castle and Phillips[11] with rats leaves the writer with the feeling that those experiments prove no more than do the experiments here reported: namely that the composition of a population may be altered by selection. It does not appear to be proven that selection has essentially altered the constitution of the germ-plasm of any particular individual as compared with the germ-plasm of that individual's ancestors, making due allowance of course for the phenomenon of segregation. That selection can alter the composition of a population with respect to genetic determiners, by a process of sorting over what is already there and rejecting some portion, no one can doubt. But it still appears to the writer to be true that: "It has never yet been demonstrated, so far as I know, that the absolute somatic value of a particular hereditary factor or determinant (*i. e.*, its power to cause a quantitatively definite degree of somatic development of a character) can be changed by selection on a somatic basis, however long continued."[12]

---

[10] I am, of course, referring to the high line selections only, merely for the sake of verbal economy. The same reasoning *mutatis mutandis* applies to the low lines.

---

[11] Castle, W. E., and Phillips, J. C., "Piebald Rats and Selection," Carnegie Institution of Washington Publication No. 195, 1914.

[12] R. Pearl, *Jour. Exp. Zool.*, Vol. 13, p. 264, 1912.